

The role of microbial mats during primary succession in calcareous dune slacks: an experimental approach

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Abstract. Laminated microbial mats from a sandy beach plain were grown in water-saturated pots in a glass house for six months and then used to assess their effect on the establishment of juveniles of three plant species representing different successional stages in dune slack development. The selected species were *Samolus valerandi*, characteristic of pioneer stages, *Calamagrostis epigejos*, characteristic of more productive, late successional stages, and *Juncus alpinoarticulatus*, which occurs in a wide range of successional stages.

Juveniles of all three species that were placed on top of intact living microbial mats established themselves in the mat. *C. epigejos* and *J. alpinoarticulatus* survived for several weeks but later on their numbers decreased and the total biomass production of the species after six months was poor. *S. valerandi*, in contrast, grew profusely in intact microbial and algal mats. Heating of the microbial mat by heat sterilization, prior to the experiment, did not improve the performance of the species.

When the juveniles were planted in the microbial mats after breaking the surface of the mat, the survival of juveniles of *C. epigejos* and *J. alpinoarticulatus* was much higher and so was the biomass of surviving plants after six months. Planting of *Samolus* in the mats had some positive effect on the survival percentage of the juveniles, but not on the total biomass at the end of the experiment. Slightly lower water tables had a negative effect on the performance of all species.

Measurements of the pH in the pots revealed that there were no significant differences in the top layer. Sulphide concentrations were very low in all the pots where juveniles had been planted and also in the pots with *S. valerandi*. Relatively high concentrations (30 - 50 $\mu\text{mol/l}$) were found in pots with poor growth of *Juncus* and *Calamagrostis* plants. These values may exceed toxic levels for these species. Although oxygen concentrations in the pots were generally low, no relation existed between plant biomass and oxygen content, indicating that plant growth was not primarily limited by oxygen stress.

These experiments support the idea that microbial mats may assist in extending the life span of early pioneer stages during dune slack succession by inhibiting the growth of species of later successional stages.

Keywords: *Calamagrostis epigejos*; *Juncus alpinoarticulatus*; Radial oxygen loss; *Samolus valerandi*; Sulphide toxicity.

Nomenclature: van der Meijden et al. (1990) for phanerogams; Schaminée et al. 1995 for syntaxa.

Introduction

Primary succession in dune slacks can be roughly divided into four phases: (1) a phase in which microbial mats and algae are dominating and where accumulation of organic material is low; (2) colonization by phanerogams which are adapted to low nutrient availability; (3) development of a moss layer of pleurocarpic bryophytes and invasion by tall grasses and shrubs, (4) rapid accumulation of organic matter, partly due to acidification of the top layer which leads to replacement of non-competitive plant species by shrubs and trees (Jones & Etherington 1992; Olf et al. 1993; Sival 1996). Many endangered dune slack species, such as *Parnassia palustris* and many orchid species as *Liparis loeselii*, *Epipactis palustris*, *Dactylorhiza incarnata*, *Herminium monorchis* and *Gymnadenia conopsea* are most abundant in the stages (2) and (3) of dune slack succession (Jones & Etherington 1992; Jones et al. 1995; Lammerts et al. 1995).

The present paper addresses the possible role of microbial mats on vegetation development in the colonizing stages of fresh water dune slacks.

Benthic filamentous cyanobacteria and algae are most abundant in tidal flats and salt marshes but they also occur in fresh water dune slacks. When growth leads to the formation of visible layers these are called microbial mats. Recent research suggests that in fresh water dune slacks these microbial mats may assist in retarding the natural vegetation succession and thus extending the life span of early pioneer stages with rare orchids (Lammerts et al. 1995).

Prerequisites for the growth of microbial mats are the availability of water and light, and the absence of excessive erosion and consumption by animals. Optimal growth conditions occur on bare soils which are regularly flooded or attain sufficient moisture by capillary water supply (Hoffmann 1942; Bauld 1984; Stal et al. 1985). Cyanobacteria in microbial mats can fix nitrogen (Stal 1985; Stal et al. 1994) and the mats may develop in a relatively short period. They may, therefore, assist in the colonization by phanerogams.

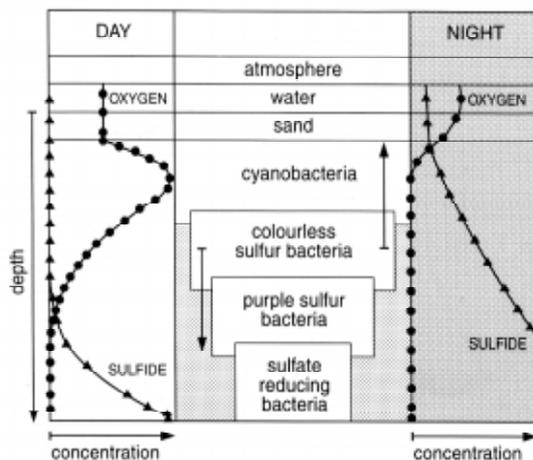


Fig. 1. Simplified scheme of a laminated microbial mat showing the diurnal fluctuations of oxygen and sulphide concentrations in relation to the vertical distribution of functional groups of micro-organisms. The dashed arrows indicate the possible migration of motile colourless sulphur bacteria to exploit the shifting gradients of sulphide and oxygen (after: van Gernerden 1993).

Cyanobacteria are also known from active blowouts (secondary dune slacks), where they can slow down erosion (Pluis & de Winder 1990; Pluis 1993). However, in these very dynamic environments susceptible to desiccation, algal crusts are predominantly ephemeral.

Knowledge of coastal microbial mats is largely derived from studies in the upper intertidal and lower supratidal reaches of sheltered sandy beaches and salt marshes (see van Gernerden 1993 for a review). Photosynthesis is concentrated in the top millimeters of the sediment, while intense respiration by heterotrophic bacteria rapidly depletes oxygen in the top layer (Fig. 1). Consequently oxygen penetration in microbial mats is shallow ranging from less than 2 mm depth in the dark to 5 - 6 mm during active photosynthesis (Visscher et al. 1991). In the absence of oxygen alternative electron acceptors, like sulphate, are used by heterotrophic bacteria in the degradation of organic matter. Well-developed mats in sulphate-rich environments are therefore characterized by an intense sulphur cycling. Sulphate reducing bacteria produce sulphide which is partly oxidized again by either phototrophic sulphur bacteria in the presence of light or by colourless sulphur bacteria when sulphide diffuses to the oxic layer.

A range of factors emerge that may influence colonization by phanerogams (for overviews see: Cohen et al. 1984; Cohen & Rosenberg 1989): 1. The mat-building organisms excrete organic extracellular polymeric substances (EPS). This changes the structure of the top soil from bare sand to a closed EPS matrix embedding

micro-organisms and sand grains. Composition of the EPS is species dependent and ranges from a gelatinous mucus to rigid intertwining extracellular sheets giving the mat a leathery structure (Decho 1994; Nicholson et al. 1987; Stal et al. 1985; Stolz 1984; Paterson 1994). 2. Sulphide concentrations may reach toxic levels for higher plants depending on the amount of available sulphate (Havill et al. 1985) and the amount of sulphide fixing iron minerals. 3. Oxygen stress may occur although the concentration of oxygen may fluctuate considerably and can rapidly change from zero to supersaturation due to oxygenic photosynthesis in the sediment (Revsbech et al. 1983; de Wit et al. 1989).

This paper focuses on the question: do microbial mats have an effect on the survival and growth of juveniles of phanerogams and if so what is the nature of this effect on the growth of early and late successional plant species?

Methods

Cultivation of the microbial mats

Undisturbed microbial mats were collected in May 1994 from an unvegetated sandy beach on the barrier island of Schiermonnikoog (53° 31' N, 6° 08' E) situated in the Dutch Wadden Sea. This sandy beach was situated in a seepage zone of the main dune massive. Fresh water was regularly discharged at the surface of the beach, particularly in the wet season (Bakker 1990; Bakker & Stuyfzand 1993). During high tides the beach was also flooded by North Sea water. The not yet fully developed mats were sampled to a depth of 6 cm using PVC tubes of 7.5 cm height and 11.1 cm Ø, which were placed in the sand and carefully removed to avoid disruption of the mats. The tubes were placed in containers in an open but sheltered glass house within 12 h. The water level in the containers was maintained at a constant (high) level ca. 1 cm below the surface. After one week each pot was provided with 1.9 mmol NH₄⁺ (as NH₄Cl), 0.073 mmol P (supplied as KH₂PO₄) and 0.015 mmol S (supplied as MgSO₄·7H₂O). This was done to speed up the development of the microbial mats.

Additional microbial mat material was taken from the same site on Schiermonnikoog in October 1994. The top cm was scraped from the sand and gathered in plastic bags. A heat treatment was carried out during 70 min. at 90 °C. The heating of the mats was carried out to ensure that the mat as a functional entity was disturbed and that biological processes that occur in actively growing mats were stopped. Empty tubes were filled up to 6 cm with sieved sand (< 0.4 mm) after which the heated material was placed on top of the sand as a 1 - 2 mm

thick layer to arrive at comparable amounts of organic matter as the fully grown mats.

In the beginning of November the pots were placed in a temperature and light-controlled greenhouse and the juveniles of the plant species were added.

Selected plant species

The selected plant species were *Samolus valerandi*, a species of early stages (stage 2) of plant colonization, *Calamagrostis epigejos*, a species of later successional stages (stage 3) with a high productivity and *Juncus alpinoarticulatus*, a species that occurs in a wide range of successional stages, but later than *S. valerandi*.

S. valerandi is a character species of the *Samolo-Littorelletum*, a wet pioneer community of low-nutrient conditions. This community is replaced during the succession by the *Junco baltici-Schoenetum nigricantis* (Westhoff 1947), a basiphilous community with many rare and endangered dune slack species such as *Schoenus nigricans*, *Dactylorhiza incarnata*, *Liparis loeselii*, *Parnassia palustris* and *Epipactis palustris*. This community is succeeded by the *Ophioglosso-Calamagrostietum*, a community dominated by the tall grass *C. epigejos* (Grootjans et al. 1988). *J. alpinoarticulatus* occurs in all three communities mentioned, but is most frequent in the *Junco baltici-Schoenetum nigricantis*.

Juvenile plants of *S. valerandi* and *J. alpinoarticulatus* were grown from seeds in petri-dishes. Juveniles of *C. epigejos* consisted of young individuals from larger plants grown from seeds in a glass house for six months. All seeds were collected in a young primary dune slack (Strandvlakte) on the island of Schiermonnikoog (53° 31' N, 6° 1' E). 10 individuals were transferred to each pot with microbial mats. Each pot with *Calamagrostis* started with three juveniles.

Treatments

During the experiment microbial mats were kept under different conditions: (A) actively growing microbial mats under waterlogged (but not flooded) conditions, (B) actively growing mats under 'moist' conditions, where the water level was 1,5 cm below the soil surface, (C) heat-sterilized mat material (which later developed a layer of green algae), kept under waterlogged conditions, (D) heated mat material kept under 'moist' conditions, (E) actively growing mats in which the juveniles were planted by breaking the mats with a small pin. Except for treatment E, juveniles were placed on top of the mats without disturbing the surface. Glass dishes were placed over the pots of experiments A-D to prevent drying out of the juveniles. The dishes were removed after two weeks when the plant roots had

established themselves in the mat. Each 'treatment' consisted of three replicates.

The observation period was 26 weeks, after which the plants were harvested.

Measurement of abiotic conditions

Oxygen was measured polarographically with a cathode-type oxygen needle electrode (Visscher et al. 1991) connected to a calomel reference electrode via a picoammeter (Keithley model 485) equipped with a polarization unit. Electrode readings were calibrated at 100 % and 0 % air saturation, assuming a linear response. Sulphide was measured electrochemically with an Ag/Ag₂S ion-specific needle electrode connected to a high impedance mV metre and a calomel reference. Sulphide concentrations were too low to allow accurate measurements at a high spatial resolution.

Statistics

The significance of the differences in biomass production between the species after 26 weeks was calculated using a Tukey-HSD test after One-way Analysis of Variance. The biomass data were log-transformed prior to analysis, to reduce inhomogeneity of variances. Homogeneity of variance was checked using Cochran's C test. The S²- values were not log transformed.

Results

Survival of juveniles

Juveniles of *Samolus valerandi* performed well at all treatments (Table 1), although the survival was highest (over 80 %) when the juveniles were planted in the intact microbial mats. Heating the mats had no effect on *S. valerandi* survival compared to intact mats, although shortly thereafter a dense mat of green algae had developed. A large proportion of the juveniles, however, perished in pots with a slightly lower water level ('moist' pots). After 10 weeks less than 50 % of the plants had survived in the 'moist' condition, while the survival in the waterlogged, further called wet pots, was well over 80 %.

The survival of *Juncus alpinoarticulatus* was low in all treatments. This effect was visible after 4 weeks when a steep fall in survival occurred in both the wet and the moist treatments. The survival was highest in treatment E in which the juveniles had been planted in the mats.

Calamagrostis epigejos juveniles declined in the pots with intact microbial mats only after 9 weeks, the survival being better in the wet than in the moist pots. The decline

Table 1. Percentage survival of seedlings of three dune slack species grown under various treatments of microbial mats: A = active mat, wet; B = active mat, moist; C = heated mat, wet; D = heated mat, moist; E = active mat, juveniles planted.

Treatment	Weeks	1	6	11	16	21	26
A <i>Samolus</i>	Mean	100.0	92.7	86.7	72.7	66.7	66.7
	S.E.	0.0	10.3	10.5	17.1	17.6	17.6
B <i>Samolus</i>	Mean	100.0	78.0	46.7	44.7	41.3	40.0
	S.E.	0.0	20.4	16.3	15.1	20.7	22.4
C <i>Samolus</i>	Mean	100.0	89.3	80.0	69.3	66.7	66.7
	S.E.	0.0	12.8	16.9	18.3	21.3	21.3
D <i>Samolus</i>	Mean	100.0	73.3	38.7	33.3	35.3	36.7
	S.E.	0.0	19.5	9.2	11.8	11.3	9.8
E <i>Samolus</i>	Mean	100.0	97.0	86.0	84.5	85.5	84.5
	S.E.	0.0	7.3	16.4	20.1	21.4	21.1
A <i>Juncus a.a.</i>	Mean	100.0	66.7	14.7	3.3	3.3	3.3
	S.E.	0.0	29.4	11.3	4.9	4.9	4.9
B <i>Juncus a.a.</i>	Mean	100.0	72.0	11.3	0.0	3.3	7.3
	S.E.	0.0	24.6	14.6	0.0	4.9	4.6
C <i>Juncus a.a.</i>	Mean	100.0	60.0	19.3	20.0	16.7	21.3
	S.E.	0.0	36.3	14.4	14.6	12.9	18.1
D <i>Juncus a.a.</i>	Mean	100.0	59.3	3.3	0.0	0.0	1.3
	S.E.	0.0	39.0	6.2	0.0	0.0	5.2
E <i>Juncus a.a.</i>	Mean	100.0	66.0	42.0	46.5	47.5	55.0
	S.E.	0.0	34.4	24.6	20.6	19.7	19.6
A <i>Calamagrostis</i>	Mean	100.0	100.0	88.9	60.0	53.3	60.0
	S.E.	0.0	0.0	16.3	25.8	21.1	25.8
B <i>Calamagrostis</i>	Mean	100.0	100.0	73.3	31.1	33.3	33.3
	S.E.	0.0	0.0	28.7	8.6	0.0	0.0
C <i>Calamagrostis</i>	Mean	100.0	95.6	48.9	44.4	68.9	71.1
	S.E.	0.0	11.7	17.2	16.3	23.5	21.3
D <i>Calamagrostis</i>	Mean	100.0	75.6	55.6	44.4	37.8	66.7
	S.E.	0.0	40.8	43.0	34.9	35.3	76.6
E <i>Calamagrostis</i>	Mean	100.0	91.7	80.0	95.0	166.7	230.0
	S.E.	0.0	14.8	25.1	46.2	102.0	114.4

started earlier in the initially heated mats with slightly lowered water levels but less rapidly than the other two species. In the second half of the observation period some recovery occurred through the formation of tillers. A distinct increase in the number of plants was observed in pots where the plants were initially planted in the mat. Therefore, the number of surviving plants was much higher at the end of the experiment.

Table 2. Total biomass (g per individual) of three plant species grown on microbial mats under different conditions for 26 weeks. Values in the same row with different letters are significantly different.

Group	A	B	C	D	E
	Wet active mats	Moist active mats	Wet heated mats	Moist heated mats	Wet planted in mats
<i>Samolus valerandi</i>	3.81 ^{ab}	1.19 ^a	5.54 ^b	3.31 ^{ab}	2.31 ^{ab}
<i>Juncus alpinoarticulatus</i>	0.11 ^a	0.07 ^a	0.78 ^a	0.02 ^a	3.48 ^b
<i>Calamagrostis epigejos</i>	0.03 ^a	0.02 ^a	0.28 ^a	0.19 ^a	1.69 ^b

Total biomass after 26 weeks

S. valerandi performed well in all treatments; several plants reached the flowering stage. The total biomass of the species was lowest in the moist pots with intact microbial mats (Table 2) and highest in the wet pots with heated soil. Planting of juveniles in tiny holes in the mat had no positive effect on the total biomass.

Table 3. Mean values of pH, organic matter (%) and S²⁻-concentrations (µmol/l) in the pots. Values in the same row with different letters are significantly different.

Group	A	B	C	D	E
	Wet active mats	Moist active mats	Wet heated mats	Moist heated mats	Wet planted in mats
pH (H ₂ O)	8.0	8.0	7.9	8.1	7.8
S ²⁻ (µmol/l)					
<i>Samolus valerandi</i>					
Top	0	13	2	2	0
Bottom	0	20	1	1	0
<i>Juncus alpinoarticulatus</i>					
Top	6 ^{ab}	10 ^a	38 ^{bc}	44 ^c	0
Bottom	49 ^c	46 ^c	37 ^{bc}	42 ^c	0
<i>Calamagrostis epigejos</i>					
Top	9 ^a	10 ^a	46 ^b	25 ^{ab}	0
Bottom	43 ^b	43 ^b	46 ^b	33 ^{ab}	0
Organic matter (%)	3.6	2.6	2.4	3.4	2.3

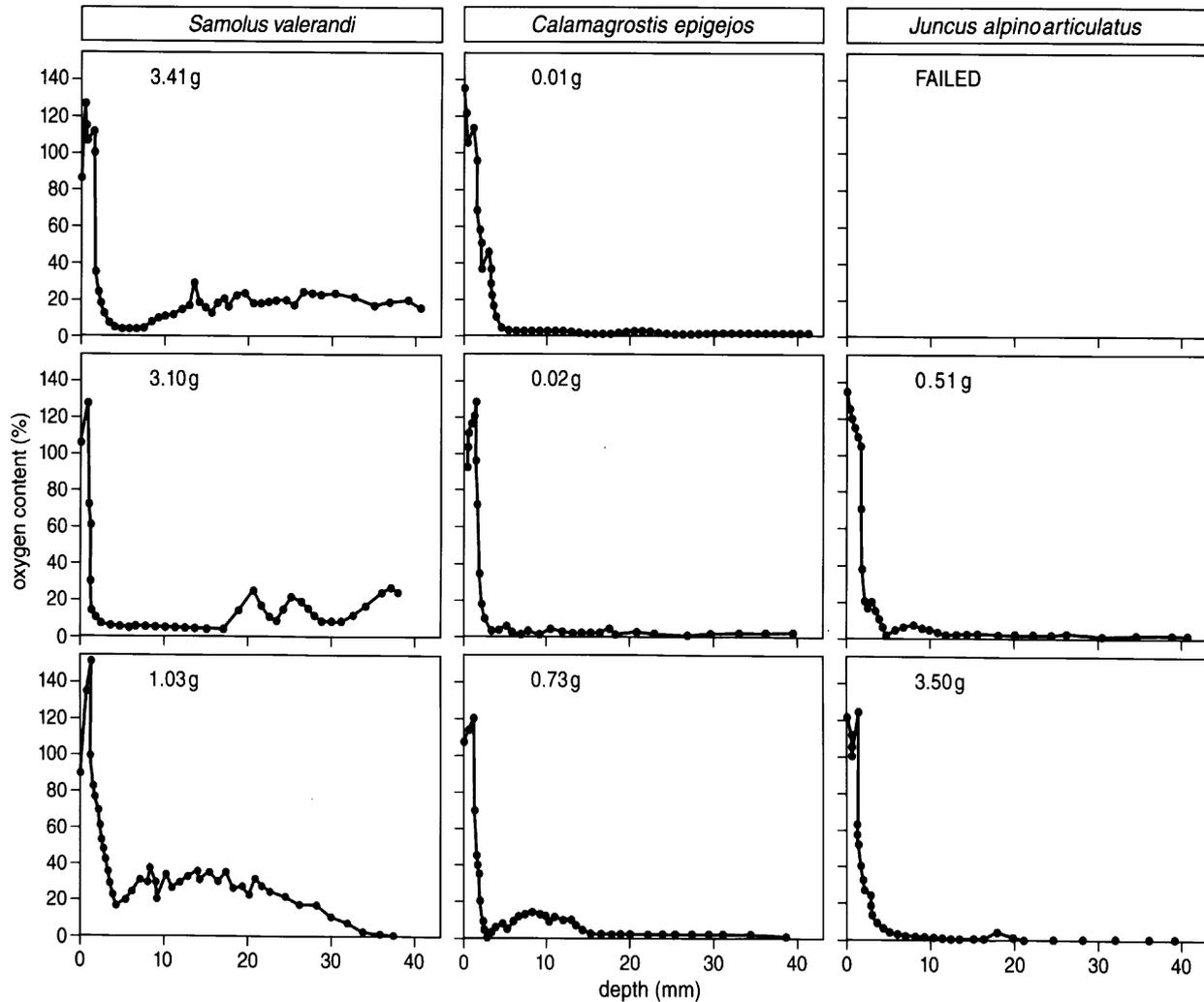


Fig. 2. Oxygen concentration in experimental pots related to the root biomass (in g per individual) of dune slack species. A = active mat, wet; C = heated mat, wet; E = active mat, juveniles planted.

Juveniles of *J. alpinoarticulatus* and *C. epigejos* did not perform very well when they were placed on top of the active or heated mats. At the end of the observation period the total biomass of the species was very low. Their growth was clearly hampered by the microbial mats or the developing layer of green algae. However, high biomass was reached if the juveniles were planted in the mineral soil beneath the mats.

Environmental conditions in the pots

Environmental conditions were equal in all pots at the moment the plants were added. Oxygen did not penetrate deeper than 5 mm into the sediment. Concentrations of free sulphide remained below the detection limit, and the pH was around 8. Environmental conditions measured at the end of the experiment are shown in

Table 3 and Fig. 2. No significant differences were found in the pH values of the top layer. The pH varied between 7.8 and 8.1 (Table 3). The oxygen content, measured in the pot profiles at every 0.2 mm, showed that oxygen was present in the first few mm of the top layers (Fig. 2). The values dropped steeply and were zero at a depth of 5 mm. Higher oxygen concentrations were measured in deeper layers (between 5 and 45 mm) of the pots in which *S. valerandi* plants were growing. Oxygen concentrations were practically zero in the deeper layers of the pots with *J. alpinoarticulatus* and *C. epigejos* plants, except for one pot with (planted) *Calamagrostis*, in which a slight increase in oxygen concentration was measured between 4 and 15 mm below the surface.

Table 3 shows that the sulphide concentrations were almost zero in pots in which *S. valerandi* plants were growing. The values were highest in the pots where *S.*

valerandi reached the lowest biomass. Low S^{2-} -values were measured in the top layer of pots with well developed microbial mats in which *Juncus* and *Calamagrostis* were poorly growing. Relatively high concentrations of sulphide were measured in the pots in which *J. alpinoarticulatus* and *C. epigejos* were growing on heated microbial mats, which later on developed mats of green algae. In these pots the S^{2-} -values were relatively high both in the top and the bottom of the pots. No sulphide was found in pots where plants were planted in the microbial mats.

Discussion

Our results show that already established microbial and algal mats inhibit the growth of *Juncus alpinoarticulatus* and *Calamagrostis epigejos*. These species performed distinctly better when they were planted in slightly disrupted mats. The pioneer species *Samolus valerandi* was not affected negatively by well-developed microbial or algal mats when grown under very wet conditions. When the water level was lowered only 1.5 cm *S. valerandi* plants performed poorly. This points to an inundation effect or to a high competition for nutrients by the microbial mats under moist conditions. It is unlikely that the growth of *S. valerandi* was restricted by oxygen stress. The measurements of oxygen content in the pots point to the ability of *S. valerandi* plants to leak oxygen from their roots (Schat 1984). Several other pioneer species of wet dune slacks, such as *Littorella uniflora* (Roelofs et al. 1984), *Schoenus nigricans* (Armstrong 1975; Ernst & van der Ham 1988; van Beckhoven 1995), are capable of leaking oxygen to the rhizosphere.

C. epigejos is a species of late successional stages in wet dune slacks, which after 10 - 25 yr gains dominance and replaces a basiphilous and low productive vegetation type with many orchid species (Westhoff 1947; Grootjans et al. 1988, 1991; Lammerts et al. 1995; van Beckhoven 1995). Van Beckhoven (1995) found that the spread of *C. epigejos* is not necessarily the result of lower water tables which may occur in later successional stages due to geomorphological changes of a barrier island or to human induced drainage. This plant species is moderately tolerant of flooding, but when the accumulation of organic matter in the top soil has reached a certain stage, the species forms a dense root system in the upper soil layer, where usually oxygen is present and in this way it is able to outcompete species such as *S. nigricans* and rare orchids.

Our experiments indicate that juveniles of *J. alpinoarticulatus* and *C. epigejos* have great difficulty to grow in already established microbial and algal mats. We can only speculate on the mechanisms responsible

for this poor growth. Although oxygen concentrations in the pots were generally low, no relation existed between plant biomass and oxygen content, indicating that plant growth was not primarily limited by oxygen stress. Low biomass was associated with relatively high sulphide concentrations, particularly in the lower reaches of the pots. Sulphide toxicity may play a role here since the roots of some plant species, such as *Stratiotes aloides*, are susceptible to sulphide at concentrations $>25 \mu\text{mol.l}^{-1}$ (Smolders 1995). Values of $>25 \mu\text{mol.l}^{-1}$ were measured at the end of the experiments in many pots with a low biomass of *J. alpinoarticulatus* and *C. epigejos*. So, apparently sufficient plant growth may prevent the production of sulphide here (Raven & Scrimgeour 1997). The poor growth of the species in pots with intact mats, therefore, may have been caused by the apparent difficulty of juvenile roots to penetrate the mats. Penetration of the mats by a small pen indeed stimulated plant growth during the second half of the experiment and this reduced the production of sulphide. In a natural situation seedlings of *J. alpinoarticulatus* and *C. epigejos* may perform better on an intact mat because germinating seeds develop roots with better capabilities to penetrate a firm soil than roots of juveniles. The next step would be to test the establishment of seedlings of a range of species in the field.

The influence of the mats would be very significant if they succeed in preventing the establishment of fast-growing phanerogams, while low-productive pioneer species remain unaffected. Furthermore, the biomass accumulation in microbial mats is low (Jørgensen et al. 1979) because a close coupling exist between the production and consumption of organic matter. Although gross primary production may be very high the mineralization of organic matter is very rapid leading to a low accumulation of organic matter. This is also favourable for pioneer species.

Microbial mats may influence the life span of early successional stages in yet another way. Calcium carbonate precipitation is well known from the marine environment of tropical to warm temperate regions, and has been associated with microbial mats and bacterial activity (Gobulic 1973; Ehrlich 1990). Chafetz (1994) recently showed experimentally that calcium carbonate crystals formed preferentially on dead remains of cyanobacteria rather than living cyanobacteria or other non-biogenic substrates. Living bacteria, however, were necessary for precipitation. The capability of promoting calcium carbonate precipitation is not restricted to marine bacteria. Relatively high calcium carbonate contents have indeed been found in early successional stages in fresh water through-flow dune slacks (Sival et al. 1997). In this way microbial mats may prevent a rapid acidification of the top soil which generally occurs in

infiltration areas with a considerable precipitation surplus. The mats are best developed in very wet slacks with ample supply of calcium and bicarbonate in the rooting zone. These conditions generally occur in dune slacks fed by calcareous groundwater exfiltrating in large hydrological systems (Stuyfzand 1993; Grootjans et al. 1996).

Concluding remarks

If microbial mats can extend the longevity of early successional stages in dune slacks, these mats, which can be distinguished in the field easily, may be used to select suitable sites for future nature conservation purposes. The mats, however are easily disrupted by car or motor tracks. Traffic on sandy beaches, which is still permitted in certain parts of the European coast, should be avoided in areas with extensive microbial mat formation.

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